Attention modulates responses to motion reversals in human visual cortex

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Selective attention modulates brain responses in visual cortex. A common finding, using functional magnetic resonance imaging or event-related potentials, is that responses to attended relative to unattended stimuli are potentiated. We report an exceptional circumstance in a motion-processing paradigm. Participants viewed superimposed stationary and moving dots and were instructed to attend to one or the other subset. Changes in the direction of dot motion triggered an event-related potential over posterior scalp sites, with a prominent negative peak at 200 ms that was larger when attention was directed at the stationary dots. This effect was localized to extrastriate visual cortex and may be due to reflexive effects of attention orienting triggered by unattended peripheral motion. *NeuroReport* 18:1361–1365 © 2007 Lippincott Williams & Wilkins.

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Introduction

The term 'selective attention' describes the ability of our perceptual mechanisms to preferentially encode, process and respond to certain attributes of the sensory environment. For example, the voice of a speaker at one location can be attended whereas voices at other locations are ignored, and the ability to make use of the information conveyed by that speaker is thereby improved [1]. Elucidating the neurophysiological basis for this phenomenon has been a goal of cognitive neuroscience since its inception. A variety of techniques have been brought to bear on the relevant questions, ranging from intracranial recordings of individual neurons to the imaging of large-scale changes in metabolic activity revealed by functional magnetic resonance imaging (fMRI). Among the most fruitful approaches has been the use of electroencephalography (EEG) and the associated stimulus-locked event-related potential (ERP). This technique measures the electrical activity generated by cortex, usually in response to the onset or change of a stimulus. A common finding in ERP studies of visual selective attention is that attended stimuli are associated with larger early ERP potentials (i.e. the P1 and N1 peaks) and this is often interpreted as increased gain on attended information, and/or sensory gating of unattended information (for reviews see Refs. [2–4]).

A common conceptualization of visual scene analysis is that the visual system encodes and represents the presence of features such as color and motion independently and then, when an object is selected by attention, it binds these representations into coherent objects [5]. For example, a substantial body of evidence indicates that the human visual pathways include regions in extrastriate visual cortex, known as MT/MST, that are sensitive to motion in the visual field [6–8]. An onset, acceleration and/or change in direction of motion has been shown to trigger robust ERP signals [9,10], and studies employing EEG source analysis [11] and its magnetic counterpart magnetoencephalography [12] suggest that motion-induced activity in MT/MST contributes to these motion-evoked potentials measured at the scalp.

The activity of MT/MST is believed also to be modulated by attention. O'Craven and colleagues [13] simultaneously presented participants with moving and stationary dots. Observers were instructed to attend to one set of dots in alternating 20-s epochs. Although motion was continuously present in the display, fMRI revealed that area MT/MST experienced alternating increases and decreases in blood flow corresponding to the attentional selection of the moving or stationary dots, respectively. This suggests an increase in metabolic activity in that region while the observers were attending to the moving dots and/or a decrease while they attended the stationary dots. In related studies [14,15], employing a transparent motion paradigm developed by Valdes-Sosa and colleagues [16], observers viewed two superimposed fields of dots rotating coherently in opposite directions. The trajectory of one of these fields changed unpredictably and the N200 ERP peak associated with this change was larger when the attended dots shifted, relative to when the unattended dots shifted. Source analysis [17] suggests that this reflects an attentional modulation of the responses of neurons in or near-area MT/MST.

We sought to examine the effect of attention on the ERP associated with changes in direction of motion in a

paradigm very similar to that of O'Craven and colleagues – we examined the ERP associated with reversals in the direction of radially moving dots while observers attended either to these moving dots, or to concurrently visible and interspersed stationary dots. We report here an unexpected result: the N200 peak associated with motion reversals was potentiated when attention was focused on the stationary rather than the moving dots.

Methods

EEG data were collected from 25 undergraduates at The University of Lethbridge who participated for course credit. Of these, data from 10 were excluded owing to their inability to maintain eye fixation in the presence of moving stimuli. Thus data from seven men and eight women (two left-handed, average age 23, normal or corrected to normal vision) were included in the analyses. Procedures were in accordance with the Declaration of Helsinki and were approved by the University of Lethbridge Human Subjects Review Committee; all participants gave written informed consent.

Participants were seated in a dimly lit room at 57 cm from a 16 inch raster-scan computer monitor set to refresh at 75 Hz with a resolution of 1024×768 pixels. A central fixation cross was always present and the participant was encouraged to maintain fixation during trials. Each trial began with the onset of a field of 78 stationary dots after a random (rectangular distribution) interval of 500–1000 ms. Half of the dots were black and half white (on an intermediate grey background). After 4 s, a verbal cue was presented via computer speakers to attend to either the white or black dots. The order of these cues was pseudorandom such that each condition occurred the same number of times in the session. Three seconds after the offset of this cue, either the black or white dots began to drift inward – toward the central fixation point – for 1000 ms and then reversed direction to drift outward. Dots drifted at $2.73°/s$ and were 100% coherent in the sense that all moving dots drifted together either toward or away from the central fixation point. The dots continued to reverse direction every 1000 ms for a total of six direction reversals. Each of these 7-s long trials was repeated four times per block in 10 blocks for a total of 240 reversals. Participants were encouraged to take a break every four blocks.

The electroencephalogram was recorded with a 500 Hz sampling rate at 128 sites using Ag/AgCl electrodes in a geodesic net (Electrical Geodesics Inc., Eugene, Oregon, USA). Electrode placement was recorded with a Polhemus Fast-Trak (Polhemus, Colchester, Vermont, USA) for later registration with the EEG dataset. Impedances were maintained below 50 kΩ. The montage was initially referenced to the vertex and subsequently to the average reference. The data were imported into the BESA software package (Megis Software, Grafelfing, Germany) for further analysis. The EEG was filtered with high-pass (1.6 Hz, 6 dB/octave) and low-pass (30 Hz, 12 dB/octave) zero-phase Butterworth filters. The record was visually inspected offline for bad channels and the signal from a small number of electrodes (approximately five or fewer per participant) was replaced with interpolated signal.

Following automatic rejection of trials contaminated by eye-movement artifact, the ERP was computed by averaging the EEG in a 1200 ms window, with a 200 ms prestimulus baseline, time-locked to motion reversals. Data were averaged across the two levels of the attended color (black or white) such that waveforms were computed for two conditions: attention to moving dots and attention to stationary dots – with 480 reversals in each condition. Data from each participant were interpolated to a standard 81-electrode montage based on the 10–20 system [18] to minimize discrepancies in electrode placement across participants, and then grand-averaged. The N200 components in both conditions were identified as a prominent negative peaks maximal over posterior scalp sites in the 210–230 ms latency range, and mean amplitudes within this time window were compared with a two-tailed t-test at the POz electrode. Difference waves were computed by subtracting the unattended reversal ERP from the attended reversal ERP, and isopotential voltage maps were computed for the difference-wave peak at 220 ms.

It is desirable to know the precise brain structures in which attention acts on motion processing. We applied electrical source analysis (BESA) to the 20 ms window centered on the N200 peak. Because of well-known limitations in spatial resolution, this technique is best applied in conjunction with a priori knowledge of the functional anatomy of the visual system. We thus took two complementary approaches in applying source analysis. First, we allowed the software to fit a current source in each hemisphere, subject to the constraint that the pair be symmetric about the sagital plane. In this model-fitting procedure, the software seeks the configuration of virtual current sources that best accounts for the measured scalp voltages. In this approach, the obtained current sources should be thought of as representing signal generated by a neighborhood of adjacent and related brain areas. Second, we asked whether area MT, known to respond to moving stimuli, contributed to the observed effect. In this approach, we fixed sources at the average stereotactic (Talairach) coordinates of area MT obtained from a recent fMRI study of motion processing [19] (left hemisphere: −47, −76, 2; right hemisphere: 44, −67, 0). Furthermore, we applied a multiple source probe scan (MSPS) [11,20] to test whether MT sources alone could account for observed effects. This technique iteratively scans a regional current source through the intracranial volume and indicates regions in which the presence of an additional source would substantially improve the model. If effects of attention are confined to bilateral MT, then two criteria should be met: the residual variance for such a model should be low (i.e. less than 10%) and MSPS should not suggest any additional contributing regions.

Results

Reversals of the direction of dot motion elicited robust ERP consistent with previous studies (Fig. 1b), with a prominent positive peak around 150 ms followed by a prominent negative peak at about 220 ms (the N200), both maximal at POz. The N200 was larger in the unattended reversals condition [t_{14}(two-tailed)=2.649; P=0.019], that is, attention directed to the stationary dots led to a larger evoked potential elicited by changes in the direction of unattended moving dots. This difference was maximal over posterior mid-line scalp sites with a polarity reversal evident over the right temple, suggesting the predominance of a right-hemisphere generator (Fig. 1a).
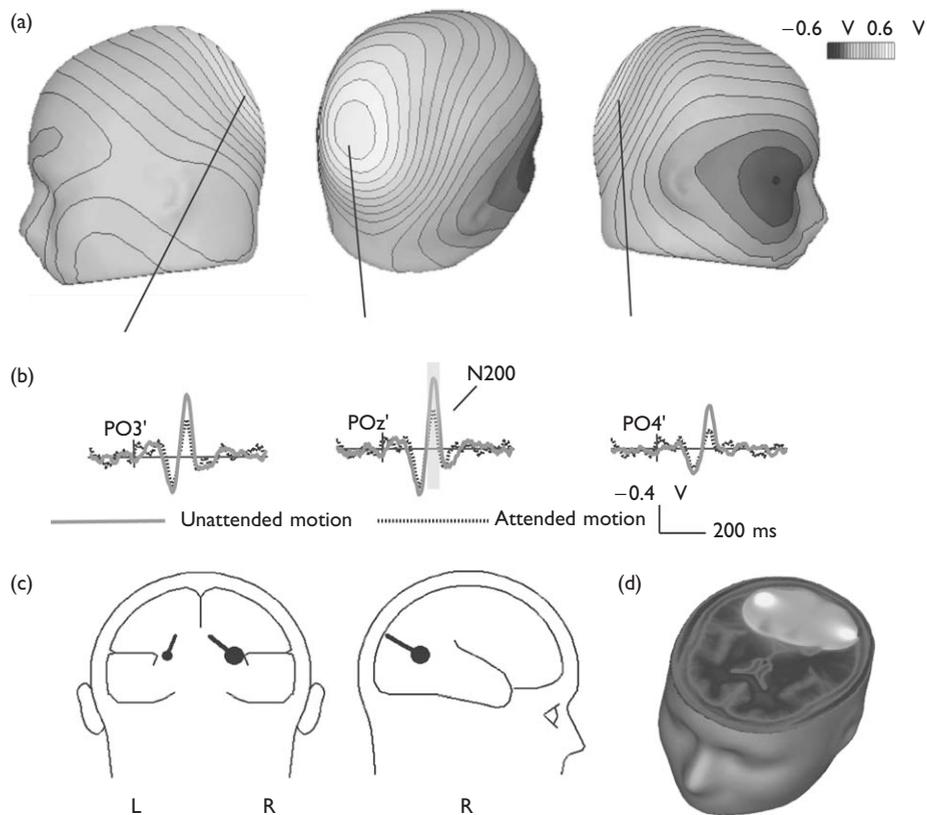
Fig. 1 (a) Isopotential voltage maps of the difference (attended minus unattended) between attended and unattended motion reversals at the 220 ms peak. This peak was maximal over midline posterior sites with a polarity reversal over the right temple. (b) ERP waveforms for attended (dotted) and unattended (solid) motion reversals at selected sites. (c) Approximate locations of equivalent current dipoles accounting for the difference between attended and unattended reversals. A pair of extrastriate generators, stronger in the right hemisphere, best accounted for the observed voltage topography. Fitting window is indicated in (b, d). The result of a multiple-source probe scan with current sources fixed in bilateral area MT superimposed on the Montreal Neurological Institute representative brain. Light areas indicate high likelihood that this region contributes signal to the ERP. ERP, event-related potential.

Bilaterally symmetric current sources were fitted to the attended minus unattended difference wave over a time window spanning ± 10 ms about the 220 ms peak (Fig. 1c). This yielded generators at approximate Talaraich coordinates ± 25.7, -63.3, 8.4, which explained 96.6% of the scalp topography. The peak magnitude of the right hemisphere dipole (-5.12 nAm) was greater than that of the left hemisphere dipole ($+2.15$ nAm). Current sources fixed solely in area MT were a poorer model, explaining 87.8% of this variance. The MSPS analysis indicated additional current generators in dorsal extrastriate visual cortex and or inferior parietal lobe (Fig. 1d).

Discussion

Investigations into modulation of brain activity by attention have converged on a common inference: that attention acts to enhance or potentiate responses to attended relative to unattended stimuli. In both the auditory and the visual system, this is typically manifested as larger peaks in the ERP and increased blood flow within these pathways revealed by fMRI. The present result that attention to stationary dots increases the ERP associated with moving dots represents an exception to this trend and is therefore of considerable theoretical interest. We consider first the implications of differences between our study and previous approaches, and then suggest two possible explanations.

The paradigm used here most closely resembles that of O'Craven and colleagues [13] in that attention was alternated between stationary and moving stimuli. In their study, attention to motion increased blood flow (and presumably neural activity) in motion-sensitive visual regions. There are two important differences: first, there are substantial differences between EEG and fMRI. Whereas EEG measures rapid changes in graded potentials at pyramidal cell bodies, fMRI measures slower changes in blood oxygenation resulting from generally increased cortical activity. Thus the fMRI and ERP results are not contradictory: it is possible that ERP would reveal a brief transient potentiation of the N200 peak for attention to stationary dots, whereas fMRI finds slow increases in blood flow when attention is directed at moving dots. Second, O'Craven et al. scanned only a 35-mm-thick section of cortex parallel to the calcarine fissure whereas the EEG technique used here more broadly captures brain electrical activity. It is possible that whole-brain imaging in their study would have revealed other regions that experienced increases in blood flow when attention was directed to the stationary dots.

The transparent motion paradigm used in related ERP studies [14–17] differs from the O'Craven et al. paradigm in

that both sets of dots are in motion. The unexpected result reported here may arise only when attentional effects are juxtaposed between stationary and moving stimuli. Indeed, one study (Ref. [15], see Fig. 1b) included a stationary baseline condition in which only a subset of dots moved. In this condition, motion onsets triggered slightly larger N200 peaks when attention was directed at dots that remained stationary.

With these differences in mind, we consider two possible explanations of the present data. One possibility is that the field of stationary dots underwent an illusory induced motion that changed direction along with the moving dots. The phenomenological appearance of this display, however, does not support this view as the stationary dots do not appear to move. In fact, a commonly reported percept was that many or all of the stationary dots vanished when the moving dots changed direction.

Valdes-Sosa and colleagues [15,16] have argued that the motion-onset ERP effects observed in previous studies are driven by a reflexive segregation of the sheet of moving dots as a new perceptual object. Similar displays capture attention when the moving elements elicit the percept of a new object as separate from the background [21]. This reflexive segregation appears to occur in our display as the moving and stationary dots perceptually resolve into distinct surfaces at motion onset. The difference in this study is that the ERP reported here was triggered by successive direction reversals of ongoing motion rather than the onset of motion. Can the reflexive object-based attention account proposed by Valdes-Sosa *et al.* nevertheless account for the present results? We suggest that the large N200 observed here in the attend stationary condition indeed reflects the same reflexive attentional process. When attention is directed at the moving dots, these dots segregate into a coherent sheet at motion onset, and then remain segregated throughout the duration of the display. As the sheet is already a segregated perceptual object when successive motion reversal occurs, no new objects segregate from the display and the N200 is thus small. In contrast, when attention is sustained on the stationary dots, both fields segregate upon motion onset, but the stationary dots become the foreground stimulus. The sheet of moving dots loses its coherence as an object because attention is focused on the stationary dots. With each motion reversal, however, a reflexive reconfiguration of this percept is triggered. As the initial representation of the moving dots has been lost, this motion signal effectively indicates the onset of a new perceptual object – despite the fact that the unattended elements had been in motion before the reversal. This situation is best thought of as a competition between a top-down goal to sustain attention on a low-salience static object and a bottom-up signal to orient to a highly salient moving stimulus.

The results of electrical source analysis, taken together, suggest that the attention effect on the N200 is not simply a modulation of activity in area MT. When allowed to fit two sources with only the constraint of symmetry, the algorithm converged on a model that explained 96.6% of the signal, but these sources were situated about 2-cm medial and dorsal to area MT. Sources fixed in area MT explained 87.8% of the data, indicating that this region likely contributes to the observed scalp distribution, but additional sources are also probable. MSPS revealed that these sources are most likely in dorsal visual cortex or parietal lobe.

Conclusion

A substantial body of previous work suggests that a neural consequence of focused attention is the enhancement or upregulation of neural activity in sensory specific cortical regions. The results reported here suggest that the ERP correlates of such enhancement are sensitive to seemingly subtle changes across different paradigms. A salient stimulus event, such as changes in the direction of unattended moving stimulus elements, can trigger robust ERP that interact with the attentional set of the viewer in complex ways.

Acknowledgements

References

1. Broadbent DE. Listening to one of two synchronous messages. *J Exp Psychol* 1952; **44**:51–55.
2. Mangun GR, Hillyard SA, Luck SJ. Electrocortical substrates of visual selective attention. In: Meyer DE, Kornblum S, editors. *Attention and performance XIV*: Synergies in experimental psychology, artificial intelligence, and cognitive neuroscience. Cambridge, MA: MIT Press; 1993. pp. 219–243.
3. Luck SJ, Woodman GF, Vogel EK. Event-related potential studies of attention. *Trends Cogn Sci* 2000; **4**:432–440.
4. Harter MR, Aine CJ. Brain mechanisms of visual selective attention. In: Parasuraman R, Davies DR, editors. *Varieties of attention*. London: Academic Press; 1984. pp. 293–321.
5. Treisman AM, Gelade G. A feature-integration theory of attention. *Cognit Psychol* 1980; **12**:97–136.
6. Tootell RB, Reppas JB, Kwong KK, Malach R, Born RT, Brady TJ, *et al*. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J Neurosci* 1995; **15**:3215–3230.
7. Zeki S, Watson JD, Lueck CJ, Friston KJ, Kennard C, Frackowiak RS. A direct demonstration of functional specialization in human visual cortex. *J Neurosci* 1991; **11**:641–649.
8. Watson JD, Myers R, Frackowiak RS, Hajnal JV, Woods RP, Mazziota JC, *et al*. Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb Cortex* 1993; **3**:79–94.
9. Clarke PG. Comparison of visual evoked potentials to stationary and to moving patterns. *Exp Brain Res* 1973; **18**:156–164.
10. MacKay DM, Rietveld WJ. Electroencephalogram potentials evoked by accelerated visual motion. *Nature* 1968; **217**:677–678.
11. Probst T, Plendl H, Paulus W, Wist ER, Scherg M. Identification of the visual motion area (area V5) in the human brain by dipole source analysis. *Exp Brain Res* 1993; **93**:345–351.
12. Ahlfors SP, Simpson GV, Dale AM, Bellivean JW, Lin AK, Korrenoja A, *et al*. Spatiotemporal activity of a cortical network for processing visual motion revealed by MEG and fMRI. *J Neurophysiol* 1999; **82**: 2545–2555.
13. O'Craven KM, Rosen BR, Kwong KK, Treisman A, Savoy RL. Voluntary attention modulates fMRI activity in human MT-MST. *Neuron* 1997; **18**:591–598.
14. Khoe W, Mitchell JF, Reynolds JH, Hillyard SA. Exogenous attentional selection of transparent superimposed surfaces modulates early event-related potentials. *Vision Res* 2005; **45**:3004–3014.
15. Valdes-Sosa M, Bobes MA, Rodriguez V, Pinilla T. Switching attention without shifting the spotlight object-based attentional modulation of brain potentials. *J Cogn Neurosci* 1998; **10**:137–151.
16. Valdes-Sosa M, Cobo A, Pinilla T. Attention to object files defined by transparent motion. *J Exp Psychol Hum Percept Perform* 2000; **26**: 488–505.
17. Rodriguez V, Valdes-Sosa M. Sensory suppression during shifts of attention between surfaces in transparent motion. *Brain Res* 2006; **1072**:110–118.

18. American Electroencephalographic Society. Guideline thirteen: guidelines for standard electrode position nomenclature. American Electroencephalographic Society. *J Clin Neurophysiol* 1994; **11**: 111–113.

19. Dumoulin SO, Bittar RG, Kabani NJ, Baker CL Jr, Le Goualher G, Pike G, Evan AC, *et al*. A new anatomical landmark for reliable identification of human area V5/MT: a quantitative analysis of sulcal patterning. *Cereb Cortex* 2000; **10**:454–463.

20. Scherg M. Functional imaging and localization of electromagnetic brain activity. *Brain Topogr* 1992; **5**:103–111.

21. Hillstrom AP, Yantis S. Visual motion and attentional capture. *Percept Psychophys* 1994; **55**:399–411.